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ADAPTATIONS TO AQUATIC, ARBOREAL, FOSSORIAL AND CURSORIAL HABITS IN MAMMALS.

IV. Cursorial Adaptations.

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Of all portions of an animal's body to undergo specialization, those which have to do with locomotion show perhaps the most varied adaptations. Speed is so essential to a great number of forms, either for escape from the enemy or for the chase of prey, that its degree of development has much to do with the fitness of the creature for survival. This adaptation is most manifest in the modifications undergone by the feet and limbs, and to a less extent in the lengthening of the head and neck in long limbed forms as a necessary correlation. Speed adaptation is further shown in the moulding of the contour of the body to lessen the resistance of the air, an increase in the capacity of the heart and lungs to meet the more rapid expenditure of energy, and finally in saltatorial forms an increase in the length and weight of the tail.

Most terrestrial mammals can run; but in comparatively few orders is there any special adaptation for speed. Offensive flight

occurs among predaceous mammals such as the carnivorous marsupials and the true Carnivora, while defensive flight is found among herbivorous forms both among the marsupials and in the placental orders Rodentia, Perissodactyla, and Artiodactyla.

Feet and Limbs : — The main foot adaptations are shown in the passage from a primitive plantigrade to a digitigrade or to an unguligrade condition, and in the reduction of the number of digits ; the last being often accompanied by a close apposition or even by a fusion of the remaining bones of the metacarpus or metatarsus, and a reduction of the number of bones in the wrist and ankle. Cursorial adaptation leads to the formation of true ginglymoid joints in the carpus and tarsus, the motion being limited to flexion and extension though the angle of movement is increased. This motion is confined to the proximal podials, while the distal ones become flat and may either fuse with each other as in the Pecora, or with the metapodials as in the Tragulidæ. The development of tongue and groove joints mars the efficiency of the limb for other purposes than running.

The laws which govern digital reduction among vertebrates lead to an interesting grouping of the Mammalia with the Amphibia in which the order of reduction is first digit I then digit V as contrasted with the Sauropsida, the reptiles and birds in which the fifth digit is invariably the first to disappear, followed by digit I.

The axis of the mammalian foot may lie in digit III as in the perissodactyls and in most rodents though not in the Leporidæ ; between digits III and IV as in the Artiodactyla and Carnivora, or in digit IV as in the diprotodont marsupials.

Another marked cursorial adaptation is the increase in length of the lower leg and foot both absolutely and in relation to the length of the femur ; the lengthening of the limb increases the stride while the raising of its centre of gravity quickens the motion. This modification reaches its highest expression in creatures of moderate size such as the medium sized antelopes for in larger animals the increase in weight demands greater structural strength which limits the degree of such elongation.

The Carnivora whose need of cursorial adaptation, outweighed by a greater need of varied motion, is less than that of other

orders under consideration show the most generalized condition of feet and limbs ranging from the ancestral canid Cynodictis of the Oligocene and lower Miocene, in which both manus and pes are pentadactyl, though with functionless pollex, to Lycaon in which structural tetradactyly prevails. In most of the Canidæ the digital formula is manus 5, pes 4; the former being however functionally tetradactyl. A curious reversional condition is seen in many high bred domestic dogs in which a functionless hallux is present without skeletal connection with the rest of the pes, similar to the dew claws of cattle. The author has invariably observed this hallux claw in Saint Bernard dogs since he first noticed it, and it seems to occur in about fifty per cent. of fox terriers. Occasionally it is observed in other breeds but not so constantly and it probably never occurs in low bred individuals. I have recently observed a Saint Bernard with *two* hallux claws on each hind foot. Cats, with the exception of Cynælurus, the hunting leopard, are not addicted to running, as their run consists merely of a series of bounds, the creature slowing down as soon as possible, hence special cursorial modifications are hardly to be looked for outside of the genus mentioned. In Cynælurus the compact feet, poorly retractile claws and dog-like proportions and musculature show an interesting case of convergence toward the Canidæ.

As in Lycaon the hyænas have also reached a condition of structural tetradactyly, the most extreme case of digital reduction to be met with in the order.

Among the polyprotodont marsupials the Tasmanian wolf, Thylacinus, which lacks only the hallux shows thus the same digital reduction as in the majority of Canidæ though the feet are much less specialized. The diprotodont marsupials on the other hand exhibit extreme modifications both for running and jumping.

Of the diprotodont marsupials the Peramelidæ, the bandicoots, exhibit decided cursorial modifications. Disparity of size exists between the fore and hind limbs, and there is aside from this fact a further kangaroo-like reduction of the pes. The hallux is very much reduced; digit IV is on the contrary the dominant one, while digits II and III are syndactylly united to offset

digit V. In Peragale the lateral digits, except the hallux, are subfunctional while in Chœropus the pes is functionally monodactyl although not structurally so. The manus of Peragale has five digits the three median ones being functional, with III as the dominant finger, while the external digits are functionless. The ungal phalanges on II, III, and IV are long and deeply cleft. In Chœropus digits I and II are reversional, digit IV being vestigial, while II and III are functional, III being as in Peragale, the dominant one.

From the digital modification observed in the Peramelidæ to that of the kangaroos is but a step, for while in the latter the manus is more generalized the pes has reached a higher degree of specialization in the total reversion of the hallux, the plan of modification being precisely as in the bandicoots. The more generalized pentadactyl manus, which shows no cursorial modification, would seem to indicate that the bipedal gait was acquired before speed requirements were met.

The Rodentia have five or six families in which true speed adaptation occurs; one, the Leporidæ, which have a combination of cursorial and saltatorial gait, the Dasyproctidæ and Caviidæ which are purely cursorial, and the Dipodidæ and Pedetidæ which are saltatorial.

In the Leporidæ, the hares and rabbits, the gait is a curious mixture of leaping and running. The wood rabbit, *Lepus sylvaticus*, when in a full gallop progresses in a manner similar to that of most quadrupeds, while the jack rabbit, *Lepus campestris*, which is a true hare, moves by a series of bounds, irregular in length, with all of the limbs moving synchronously, though the weight borne upon the fore limbs must be very slight, the powerful hind limbs giving the impetus to the body. The Leporidæ show no especial digital modification other than the simple reduction of the hallux. There is an elongation and greater compactness of the metapodium as in the Canidæ among the Carnivora, and the axis of the foot lies between digits III and IV.

Of the purely cursorial types the Dasyproctidæ are the more generalized though they exhibit two distinct stages in the reduction of the digits. The first is that of Cœlogenys, the paca, in which the manus and pes are both structurally pentadactyl

though the pollex is reduced, while in the foot but three digits are functional, the lateral digits being vestigial.

In Dasyprocta, the agouti, however, the hand remains distinctly pentadactyl though digits I and V are subfunctional, while in the foot the digits are reduced to three. Thus the foot is both structurally and functionally tridactyl, the metatarsals being closely pressed together though not fused. The compact pes thus formed is tending toward that possessed by the Dipodidæ (*vide infra*).

The Caviidæ, represented by the Patagonian cavy, Dolichotus, show a further reduction over Dasyprocta in that in the former the manus is tetradactyl while the pes is in the same stage of reduction in each.

Among the truly saltatorial rodents a range of specialization is shown, starting from Perodipus, in which the manus and pes are each pentadactyl though there is considerable disparity of size between the fore and hind limbs, the progression being by leaping with the hind feet. Dipodomys, the kangaroo rat, belonging, together with Perodipus, to the American family Heteromyidæ, has much the same proportions, but the pes is tetradactyl. In Pedetes, the African jumping hare, the pes is tridactyl, the median digit being much the longest ; while in the true jerboas, as Dipus, the disparity between the limbs reaches its greatest development and the elongate metatarsals are fused into one very bird-like bone. The digital formula is manus 5, pes 3 ; but the clawless pollex is evidently undergoing reduction.

Among the ungulates I know of none in which cursorial adaptation is manifest, which have not already functionally lost the pollex and hallux, that is with the exception of Phenacodus among the condylarths which was pentadactyl and undoubtedly could run though exhibiting no very marked cursorial adaptation. In general, while the pes is often more specialized than the manus there is far more uniformity in the plan of modification of fore and hind feet than was observed in the rodents and diprotodont marsupials. The artiodactyl and perissodactyl stems have modified the feet in such different ways that it becomes necessary to give each group separate treatment.

Among the Perissodactyla, the rinocerotine group, mostly of

unwieldy build, contains but one family, the Hyracodontidæ, ranging in North America from the Bridger to the White River, in which a running type developed. Here the manus is tetradactyl, the pes tridactyl, and as Osborn[1] says: "Tridactylism is rapidly acquired with a tendency to monodactylism in the lower Oligocene." They strongly suggest the primitive horses in general contour.

The Equidæ are too well known to require more than a brief review. The pentadactyl ancestral form is as yet undiscovered and must be looked for in the Cretacic, for in the lower Eocene there appears Eohippus with a tetradactyl manus, the pollex being represented by a splint, and a tridactyl, elongated pes which bears a splint of digit V. The other Eocene horses exhibit the same stage of digital reduction as in Eohippus; but Mesohippus of the middle and upper Oligocene is tridactyl in the manus as well as in the pes, the fifth digit of the former showing a splint-like metatarsal, digit I being vestigial. Here all of the digits are functional the laterals finally losing their contact with the ground in Merychippus of the middle Miocene and in Neohipparion of the upper Miocene, a beautiful specimen of which has lately been added to the American Museum collection. Hypohippus of the middle Miocene with subfunctional lateral digits and, in the manus, the vestige of metacarpal V is an instance of arrested evolution owing probably to marsh dwelling habits which necessitated a spreading foot.

Finally the monodactyl type of the Pleistocene and Recent is represented by the genus Equus in which digits I and V are reversional and digits II and IV vestigial, being represented by the metapodial splints alone.

The Equidæ are curiously paralleled in foot reduction by the South American Litopterna in which the tridactyl condition with functionless lateral digits is shown in Proterotherium from the Santa Cruz formation, Lower Tertiary of Patagonia. This creature seems to parallel Merychippus, the main distinctions being that the former has rather more slender phalanges in the middle digit while those of the lateral digits are proportionately

[1] Osborn, H. F. The Extinct Rhinoceroses of North America. *Mem. Amer. Mus. Nat. History*, Vol. I, Part 3, p. 93.

more robust. The metapodials are shorter and stouter than in the horse, those of digits II and IV particularly being much more prominent.

Thoatherium from the same beds is monodactyl, the lateral metapodials being even more vestigial than in Equus which it parallels, and as in Proterotherium, the phalanges, especially the proximal and ungal of the remaining digit are much more slender than in the horse, the ungal being cleft. A curious admixture of perissodactyl and artiodactyl characters is seen in the feet of the Litopterna for they have the odd toed feet of the Perissodactyls together with the characteristic double tarsal joint, though not to so great an extent, of the artiodactyls.

The Artiodactyla early lose the hallux and pollex, for except in Oreodon and Agriochœrus we have no instance of their survival and while digits III and IV are equally well developed, II and V suffer all degrees of reduction from that seen in the swine to the total disappearance in the camel and Antilocapra.

The swine are four toed, the lateral digits being sub-functional. Dicotyles, the peccary shows an advance over most Suidæ in that digit V of the pes is entirely wanting giving an asymmetrical foot, of uncommon occurrence in the order though found in the Anoplotheres as well. In Dicotyles the metacarpals are slightly fused at their proximal end while in the metatarsals the fusion extends over half the length of the bones. The Pleistocene genus Platygonus shows a still greater specialization as it is structurally didactyl, but a splint of the fifth metatarsal remaining. The metapodial bones show a greater degree of fusion than in Dicotyles.

The Tragulidæ or chevrotains are in a sense transitional between the swine and the true deer for, while four toed, the lateral toes are functionless although in the existing genera Tragulus and Dorcatherium (Hyomoschus) the lateral metapodials are entire. Fusion of the median metatarsals to form a canon bone is found in Tragulus, but not in Dorcatherium which together with its somewhat better developed lateral digits presents a more generalized condition than does Tragulus. Gelocus, an extinct form ranging from the Eocene to the Oligocene, is more specialized than either of the existing genera in that the

lateral metapodials are incompletely ossified. The metacarpals are not fused, while the presence or absence of fusion of the metatarsals is a specific variation.

The extinct Oligocene genus Protoceras gives us an interesting example of the acceleration of the specialization of the hind limbs over the fore, for while the latter have four well developed functional digits those of the former are reduced to two only, with closely applied metatarsals which do not fuse, though strongly tending so to do. The lateral metatarsals are represented by proximal vestiges only.

In the Pecora or true deer the lateral digits are reduced, being functionless in most genera though sub-functional in Moschus and in Rangifer probably due, in the latter genus at any rate, to the necessity of a broad plantar surface for support on the mossy tundras or on the snow, a condition analogous to that of Hypohippus among the horses. In the deer the lateral metapodials are incomplete, their distal ends always occurring while only in certain genera as Cervus and Cariacus are the proximal extremities also retained.

The Bovidæ exhibit an almost complete reduction of the lateral digits, the dew claws being dermal appendages only, the proximal phalanges being invariably absent, while the final stage of total reduction of the lateral toes is found in the camels, the giraffe, and in Antilocapra. In the Bovidæ as well as in the later Camelidæ and the other forms mentioned the fusion of the metapodials to form a canon bone is complete.

In the later camels there is a retrograde descent from the unguligrade to the digitigrade condition, wherein the phalanges lie prone upon the ground, giving the characteristic broad, pad-like foot of the modern camel.

There are no instances of saltatorial adaptation among the ungulates though some antelope and deer are wonderful jumpers.

The lemurs among the primates present several instances of saltatorial adaptation, notably in the sub-family Galagininæ and in Tarsius, family Tarsiidæ ; but here instead of an elongated metatarsus, which has been the rule heretofore, it is the tarsus which is modified, for the calcaneum and navicular become

lengthened and cylindrical as do the calcaneum and astragalus in the frog. The hallux is large and opposable while digits II and III are somewhat reduced, digit IV being the longest. In Tarsius digits II and IV are clawed while the others bear flattened nails.

The Skull.— Cursorial adaptation has its effect upon the skull only in the correlation that exists between long limbs and dolichocephaly, brought about by the necessity of reaching the ground on the part of a grazing animal. This is strikingly illustrated in the horse series where the increase in the length of the skull parallels the lengthening of the limbs.

Saltatorial forms which, like Dipus, have lengthened the hind limbs only, do not exhibit marked dolichocephaly, as the feeding habits of the creature do not require it. The grazing kangaroos however have a moderately elongate skull.

The Vertebral Column.— Cursorial adaptation among mammals is shown in the lengthening of the cervical vertebræ, especially in dolichocephalic forms, strikingly illustrated by the giraffe and by Alticamelus of the Loup Fork of Colorado [1] a camel showing the most remarkable convergence toward the giraffe, although the latter is derived from a totally different stock.

Among the saltatorial forms, especially those with brachycephalic skulls, the tendency is toward the shortening of the neck accompanied by a greater or less degree of immobility. In Pedetes cervicals 2 and 3 are so closely articulated as to eliminate motion, in Perodipus the axis and the next two vertebræ are fused, while in Dipus all of the cervicals except the atlas are coössified as in whales. There is no increase or diminution in the number of cervicals as a result of speed adaptation. The dorso-lumbar series seem to suffer little alteration in cursorial forms, though the lumbars increase in size in saltatorial types. The high number of vertebræ found in the horses is also found in other perissodactyls and in the Proboscidea, and so is not to be considered a modification coming within the scope of the present discussion. In some saltatorial forms, as the jerboas, an exceedingly short back is found; but saltatorial adaptation can exist without this feature.

[1] Matthew, W. D. *Mem. Amer. Mus. Nat. History*, Vol. 1, Part 7, p. 429, pl. XXXIX.

The tail is generally reduced as a result of cursorial adaptation, though in coursing dogs, as the grayhound and pointer, it aids in keeping the balance when the creature changes its direction and this may be a secondary cause for its retention. In saltatorial forms on the contrary, the tail becomes an important organ for use as a counterpoise; for in truly saltatorial mammals the tail increases in length and in weight directly with the increase in proportion of the hind over the fore limbs. It is in such bipedal forms as the kangaroos and the jerboas that the caudal counterpoise reaches its highest expression, for in the former the tail is long and heavy while in the latter the somewhat less proportionate weight is compensated for by the extreme length of the organ and the tuft of hair at its tip. The tail of the African jumping hare, Pedetes, is long and feather-like, like that of a squirrel. The development of a caudal counterpoise in bipedal mammals is paralleled among dinosaurs of the Mesozoic though, as the author will show in a forthcoming memoir,[1] dinosaurs are never saltatorial, but always progress by alternating strides. This is what one would be led to infer, for whatever the increase in speed may be, I know of no reptile which runs at a gallop that is with each pair of limbs moving nearly in unison, while among the mammalia this is the common method of rapid progression. The jerboas *walk* on the hind limbs with alternate strides, *hopping* only when speeding while the kangaroos have lost the more primitive alternate footed gait and use the hop for all degrees of rapidity. The hop may thus be considered as a sort of bipedal gallop.

Among the struthious birds, the cursorial habit evidently having been acquired after the loss of the reptilian tail, the counterpoising function is subserved by the wings which bear up the anterior part of the body and at the same time lighten the creature's weight.

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[1] Lull, R. S., Fossil Footprints of the Jura-Trias of North America. *Mem. Boston Soc. Nat. Hist.* Vol. 5, no. 10.

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